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Production in spruce grouse: the reevaluation of a density-dependent hypothesis

by

Kathryn E. Smyth

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Date...February 11, 1983.....

Abstract

The relationships between production of spruce grouse and the density of females, their age structure, the timing of hatch, and several weather parameters before and after hatch were examined using data collected between 1965 and 1981 from a population in southwestern Alberta. Production was not correlated with timing of hatch or temperature and precipitation before and during laying and after hatch. Reanalysis of data did not appear to support the hypothesis that production was negatively related to density of females during the breeding season. Production may have been related to the proportion of yearling females in the population; however, any significant relationship between them seems to have been masked by the detrimental effects of wet weather during incubation in 2 years. Production of juveniles and the proportion of females with broods were negatively correlated with the number of days with precipitation during incubation; however, the effects of these relationships were most apparent under extreme conditions and appeared to have little influence in most years. Reduced production in years of inclement weather during incubation may have resulted from increased loss of nests due to desertion by energetically-stressed females and increased susceptability of females to predation or stress-related disease.

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Introduction

Production varies with the proportion of females breeding and their success in raising young to independence. In some tetraonids, the number of young produced in one year has been reported to influence population size the following year. This relationship appears to hold true for two subspecies of willow ptarmigan (*Lagopus lagopus*) (Bergerud 1970, Myrberget 1972), red grouse (*Lagopus lagopus scoticus*) (Jenkins and Watson 1967), and rock ptarmigan (*Lagopus mutus*) (Jenkins and Watson 1967, Weeden and Theberge 1972). Among blue grouse (*Dendragapus obscurus*), however, changes in spring population size were not associated with changes in productivity (Boag 1966), early mortality of juveniles (Zwickel and Bendell 1967), or clutch size and nesting success (Zwickel 1975) the previous year.

The number of young produced in any one year and potentially available for recruitment into the breeding population the following year can vary in response to a number of factors. Spring population density appears to influence production of young in a number of galliforms. Boag *et al.* (1979) found that production of young varied inversely with spring density of female spruce grouse (*Canachites canadensis*) and suggested that this relationship could provide one means of controlling population size (a

density-dependent hypothesis). A negative relationship between spring density and subsequent measures of production has also been reported in California quail (*Lophortyx californicus*) (Francis 1970) and willow grouse (*Lagopus lagopus lagopus*) (Myrberget 1972). By contrast, Moss *et al.* (1975) found that breeding success was not related to spring density of red grouse.

Age structure of a population may influence production if adults and yearlings differ in nesting success or brood size. Among some species of grouse, a large proportion of yearlings are suspected to be non-breeders: 30-40% in spruce grouse (Boag *et al.* 1979) and 46% in blue grouse (Hannon and Zwickel 1979). Yearling females tend to have smaller clutch sizes in rock ptarmigan (Weeden 1965), willow ptarmigan (Myrberget 1967), spruce grouse (Ellison 1974, Keppie 1975a), and blue grouse (Zwickel 1975). Thus, a combination of lower rates of breeding among yearlings and a generally lower clutch size suggests that this age class may contribute less to production than does the adult.

Timing of nesting is often viewed as an adaptation optimizing the availability of food for the young or adult bird (Immelman 1973). In temperate latitudes it tends to be under the control of photoperiod (Immelman 1971). This timing can be modified by additional proximate factors such as the physical and social conditions prevailing each year (Immelman 1973). If optimal hatching conditions and time of hatch do not coincide, production may vary with time. For

example, Ellison (1972) found that brood size in July-August decreased and number of broodless females increased among Alaskan spruce grouse in an unusually late year. However, hatch date was not related to measures of reproductive success (average clutch size, egg loss, or brood size) in two subspecies of willow ptarmigan (Bergerud 1970, Myrberget 1972, Marcstrom and Hoglund 1980).

The influence of weather before nesting and shortly after hatch on nesting success and/or juvenile survival is equivocal. Weather after hatch could not explain variations in production of blue grouse (Zwickel and Bendell 1967), ruffed grouse (*Bonasa umbellus*) (Gullion 1970), red grouse (Watson 1970), willow ptarmigan (Myrberget 1972), or rock ptarmigan (Theberge and West 1973). Bergerud (1970), although finding no general correlation between weather shortly after hatch and productivity of willow ptarmigan, did find that the coldest year had the fewest juveniles per brood and suggested that extremely cold weather may have a depressive effect on production. Cold temperature, often combined with high precipitation, after hatch was associated with poor production in blue grouse (Boag 1966), willow grouse (Slagsvold 1975, Marcstrom and Hoglund 1980), and capercaillie (*Tetrao urogallus*) (Slagsvold and Grasass 1979).

It is apparent that some or all of these factors may affect production in galliforms. I re-examined the effect of spring density of females on production, including data from

more years than were available to Boag *et al.* (1979). Based on their hypothesis, I predicted an inverse relationship between density of females and production. I examined the effect of age structure of the female population on production. In this case I expected a decrease in production with an increase in the proportion of yearlings in the female population. I examined the timing of nesting and weather during various phases of the reproductive cycle to determine whether any relationships were evident. I predicted that a delay in the onset of nesting and cold, wet weather in the immediate post-hatch period would be related to reduced production. Since evidence that weather conditions during incubation influence production is equivocal, I could not predict any relationship between those variables.

Study Area and Methods

The study area, situated in the foothills on the east slope of the Rocky Mountains, 27 km west of Turner Valley, Alberta, has been described in detail by Boag *et al.* (1979). It was extensively burned in the late 1930's and is now dominated by lodgepole pine (*Pinus contorta*) with patches of mature white spruce (*Picea glauca*) and poplar (*Populus* spp.).

The study area (Fig. 1) was subdivided into six sections (referred to as GC1 - GC6), most of which were censused between 1965 and 1981. Data for 1969, 1976 and 1977 are not included because of their incompleteness. Areas censused in the remaining years are presented in Table 1. Size of the study area and the data collected varied over the years with the research programs of different workers; data from some years are therefore unsuitable for the analyses used in this study.

Pointing dogs were used to census grouse in most years. Birds were captured using an extensible noosing pole (Zwickel and Bendell 1967a) and individually marked with colored leg bands. In 1974, 1975, 1980, and 1981 some females were equipped with radiotransmitters following the methods of Herzog (1979). Juveniles were marked with numbered wing tags (Keppie 1975b) until they became large

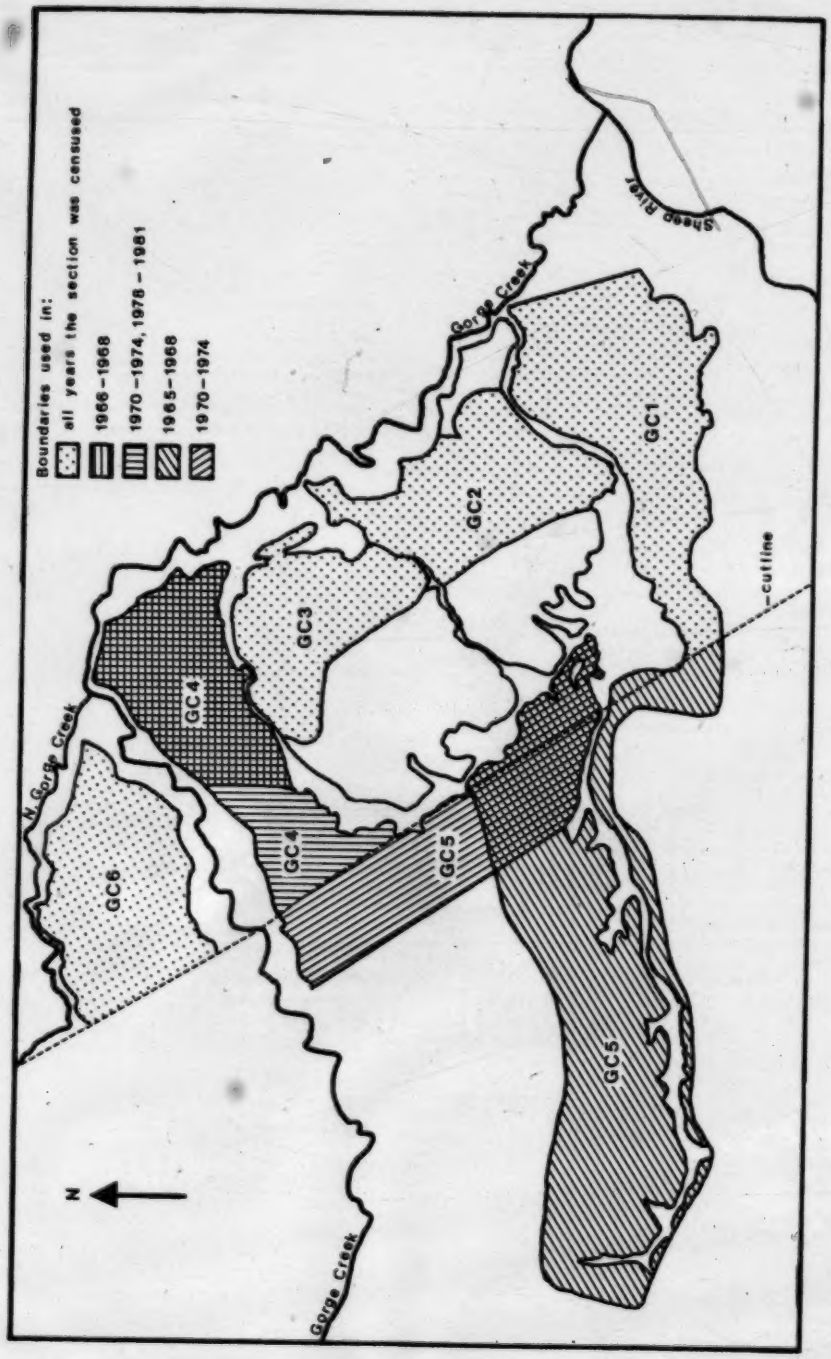

Figure 1. Boundaries of sections of the spruce grouse study area in southwestern Alberta as used in this study.

Table 1. Sections of the study area censused completely during the years 1965-1968, 1970-1975, and 1978-1981 and their respective sizes.

Section	Size (ha) of area censused in given years				
	1965	1966-1968	1970-1974	1975	1978-1981
GC1	87	87	87	87	87
GC2		60	60		60
GC3		48	48	48	48
GC4		52	73		73
GC5	212	212	73		
GC6			60		60
Total	299	459	401	135	328

enough to band at about 40 days of age. Hatch date and age of juvenile were calculated from their estimated age at capture based on length of primaries (McCourt and Keppie 1975). In spring, birds were either adults (>15 months) or yearlings (6-15 months) based on the criteria of McCourt (1969) and McKinnon (in press). Hens were considered potentially breeding residents if seen at least once between 15 May and 15 August (Keppie 1975b).

Survivorship curves (Ricklefs 1979) were constructed to determine when the major loss of juveniles occurred. Only those broods for which brood size was known within 4 days of hatch and for each 5-day period thereafter until day 40-44 were used. Number alive in each of the periods was plotted on semi-log paper for broods in which at least one juvenile was lost.

Densities of grouse over the entire study area and on each section (GC1-6) were calculated as number of females per 100 ha. Females were considered residents of those sections on which the majority (>50%) of their sightings, between 15 May and 15 August, were located. Densities were compared between years and sections.

Production was defined as the number of juveniles aged 4 or more weeks per resident female. Juveniles were considered residents of the same section as their hen. Production was calculated for each section and the entire study area. Between-section differences were examined.

The relationship between density and production, over the entire study area and on each section, was investigated. In 1965 and 1975 density could be estimated using census data from two sections only and as such may not be comparable to estimates based on five or six sections. In 1965, 1967, 1968, and 1978 brood size at age 4 or more weeks was not known for each female that had a brood. Production estimates based on incomplete data for these years were presented as a range: the upper limit assumed that all juveniles in broods seen early in the year actually survived to 4 or more weeks even though not seen at the latter age and the lower limit assumed that no juveniles survived in broods not seen after they were 4 or more weeks of age. Correlation analysis of density and production on the entire study area included only those years for which density was estimated on at least five of six sections and for which brood size at age 4 or more weeks was known for all females: 1966, 1970-1974, and 1979-1981. Estimates of production and density for 1965, 1967, 1968, 1975, and 1978, although not used in the correlation analysis, were plotted to show their general positions relative to other years. Correlation analysis of density and production for each section included only those years for which density was estimated on that section and for which brood size at age 4 or more weeks was known for all females.

Production of adult and yearling females was compared using the following data: maximum number with broods, number

with broods aged 4 or more weeks, number of juveniles aged 0-4 days and 4 or more weeks per successful female, and number of juveniles aged 4 or more weeks per resident female. For these analyses data for all years were combined. The proportion of yearlings in the population each year was compared with the number of juveniles aged 4 or more weeks per resident female.

The influence of timing of hatch on production each year was examined, in addition to two factors which may influence this timing: age of female and spring weather. First-known and median hatch dates of adults and yearlings were compared. Proportion of yearling females in the population each year was compared to median hatch date. Average daily maximum and minimum temperature, average daily precipitation, and proportion of days with precipitation were calculated for 10 weekly intervals from 1 April to 9 June for each year and compared to first-known and median hatch dates. The number of juveniles aged 4 or more weeks per resident female was then compared to median and first-known hatch dates for three groups: adults, yearlings, and all females. Proportion of females with broods was compared to median hatch date. The influence of timing of hatch on brood size was also examined by comparing number of juveniles aged 4 or more weeks per female in clutches which hatched before or on the median hatch date to those clutches which hatched after this date in all years.

Possible relationships between weather before and after hatch and three measures of reproductive success (proportion of hens with broods, brood size at age 11-19 days, and brood size at age 4 or more weeks) were examined. Weather data from Turner Valley, 27 km east of the study area, were used as representive of conditions on the study area. It was complete for the years needed and daily maximum and minimum temperature and 5-day total precipation were correlated (Pearson's product-moment correlation, for all years: $r>0.67$, $P<0.05$) with weather from Sheep River Ranger Station, about 3 km from the study area, for which records were kept only until 1975.

Average daily maximum and minimum temperatures, average daily precipitation, and proportion of days with precipitation were calculated for each of the following five periods during the breeding season.

1. Prelaying - 14 days before the first egg was laid; Hannon (1978) found that rapid recrudescence of follicles occurred over a 9-day period in blue grouse.
2. Laying - 7 days; the minimum time needed to lay an average-sized clutch of 5 eggs (Keppie 1975) at 1.4 days per egg (McCourt *et al.* 1973).
3. Incubation - 22 days; based on reports of 21 (Pendergast and Boag 1971) and 23.5 days (McCourt *et al.* 1973).
4. Early post-hatch - 1-4 days after hatch; thermoregulation is not well-developed in grouse until 5-7 days of age (Zwickel 1967, Theberge and West 1973,

Myhre *et al*. 1975, Allen *et al*. 1977).

5. Late post-hatch - 1-14 days after hatch; most mortality of grouse juveniles occurs before 14 days of age (Zwickel and Bendell 1967, Keppie 1977, Erikstad 1979).

To compare weather between years, it was necessary to choose periods of time when most hens in the population were at a particular phase in the reproductive cycle (for example laying). Because hens were not completely synchronous in the onset of reproductive events, each period encompassed the time that the first 80% of hens in the sample were involved in that activity (Table 2).

The dates in periods 1-5 were calculated by backdating from hatch dates of successful hens for most years. Based on the results of Zwickel (1977) for blue grouse, I assumed that such dates were representative of all hens in the population. For 2 years of very poor success - 1975 and 1980 - there were few hatch dates on which to base estimates of breeding events. Additional data on laying and incubation from unsuccessful radio-tagged hens were used to improve the estimates of breeding events in those years.

Table 2. Dates encompassing the time when 80% of the females on the study area were estimated to be in each phase of the reproductive cycle.

Year	Dates (day/month)				
	Prelaying	Laying	Incubation	Early post-hatch	Late post-hatch
1965	19/5-12/6	2-13/6	8/6-4/7	30/6-8/7	30/6-19/7
1966	11/5-13/6	25/5-14/6	31/5-5/7	22/6-9/7	22/6-20/7
1967	17/5-17/6	31/5-18/6	6/6-9/7	28/6-13/7	28/6-24/7
1968	16/5-15/6	30/5-16/6	5/6-7/7	27/6-11/7	27/6-22/7
1970	14/5-10/6	28/5-11/6	3/6-2/7	25/6-6/7	25/6-17/7
1971	7/5-9/6	21/5-10/6	27/5-1/7	18/6-5/7	18/6-16/7
1972	9/5-11/6	23/5-12/6	29/5-3/7	20/6-7/7	20/6-18/7
1973	13/5-8/6	27/5-9/6	2-30/6	24/6-4/7	24/6-15/7
1974	18/5-26/6	1-27/6	7/6-18/7	29/6-22/7	29/6-31/7
1975	11/5-9/6	25/5-10/6	31/5-1/7	22/6-5/7	22/6-16/7
1978	13/5-12/6	27/5-13/6	2/6-4/7	24/6-8/7	24/6-19/7
1979	7/5-8/6	21/5-9/6	27/5-30/6	18/6-4/7	18/6-15/7
1980	3-30/5	17-31/5	23/5-21/6	14-25/6	14-29/6
1981	18/5-10/6	1-11/6	7/6-2/7	29/6-6/7	29/6-17/7

Results

Survivorship of Juveniles

To determine the age at which most juvenile mortality was occurring, and thus when it was appropriate to consider counts of juveniles as representative of survival to various ages throughout the summer, a survivorship curve was constructed using counts of juveniles from those broods in which some loss had occurred (Fig. 2). The period 0-4 days after hatch was used to represent brood size at hatch. Because few broods were found on the day of hatch, it was necessary to include broods first seen up to 4 days after to obtain a workable sample size. Thus, brood size at 0-4 days probably included some post-hatch loss. About 67% of juveniles disappeared in the first 14 days after hatch. The period when broods were 11-19 days was used to reflect brood size when rate of loss was greatest. In most years, brood counts for all females in late August-early September, just prior to the time of dispersal, were not available. In order to include as many years as possible in the analyses, the number of juveniles aged 4 or more weeks per resident female was used as an index of production for each year since loss had leveled off at 78% by 25-29 days of age. The apparent drop in numbers at 40-44 days (Fig. 2) was due to the loss of three juveniles, possibly an artifact caused by handling

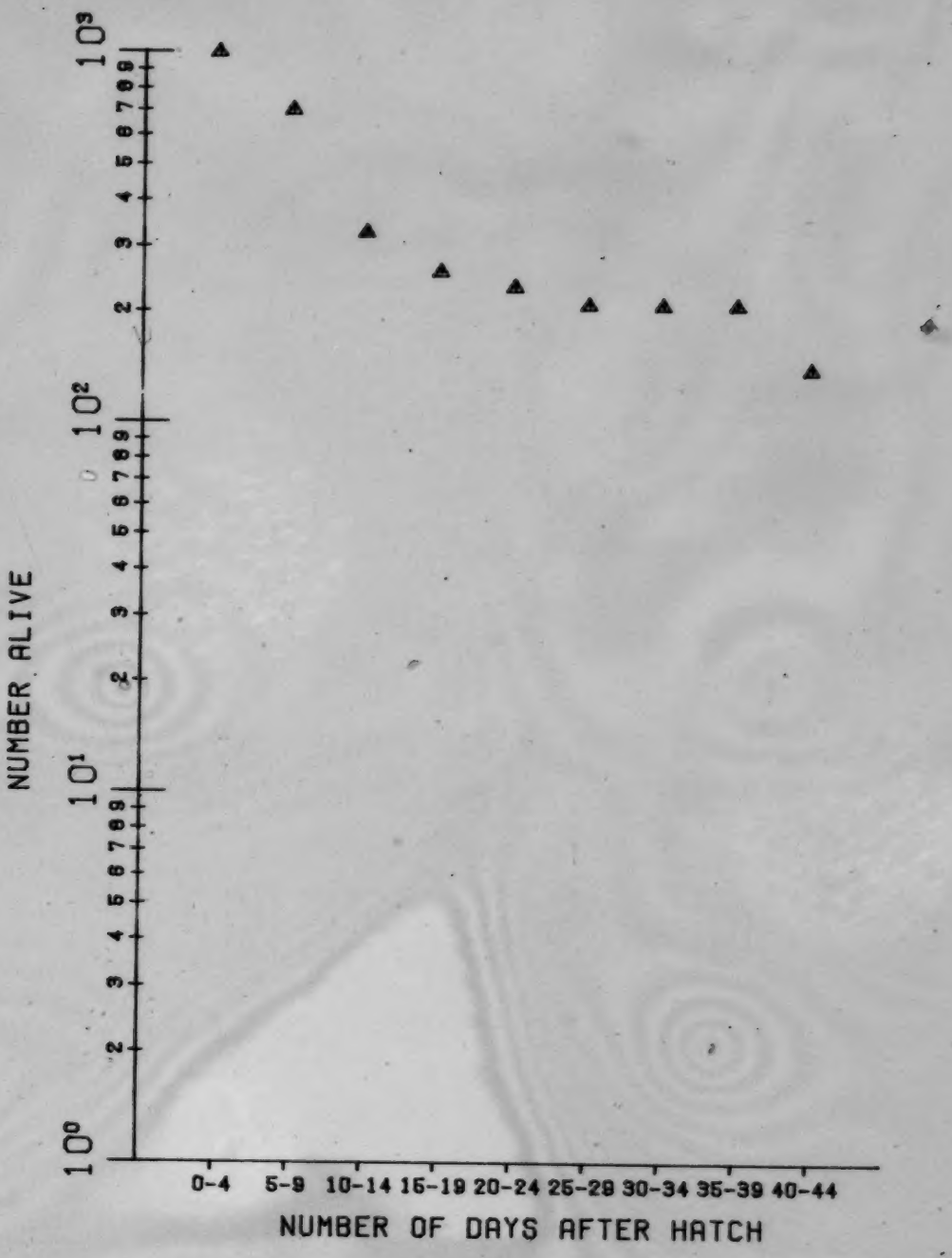

Figure 2. Survivorship of juveniles from those broods in which some loss was known to have occurred (at time 0-4 days, n=43 juveniles in 10 broods).

since that is the age at which they are large enough to band.

Density

In order to control for habitat heterogeneity, the same boundaries were set for the study area in as many years as possible. Densities in all years except 1965 and 1975, were based on a common area of 247 ha censused in each year. An additional 212 ha were added for the years 1966 to 1968; 33 ha of this were also censused in 1970 to 1974. An additional 81 ha were also censused in 1970 to 1974 and 1978 to 1981. Because the size of the study area in the years considered in the statistical analyses varied from 328-459 ha, the influence of habitat variability was only partially controlled.

The density of females on the study area differed among both years and sections (Kruskal-Wallis test, $P<0.01$; in both cases) (Table 3). The latter difference can be attributed to GC3 which had higher densities than GC1 (pairwise contrasts of Kruskal-Wallis test, $P<0.05$); however, neither differed significantly from the other sections. Because of the difference in density among years it was possible to consider the influence of changing density on productivity.

When production was plotted against density of females on the entire study area (five or six sections depending on the year) no correlation was evident (Spearman's $r=0.051$,

Table 3. Density of female spruce grouse on sections of the study area for the years 1965-1968, 1970-1975, and 1978-1981.

	Number of females per 100 ha in given sections						
Year	GC1	GC2	GC3	GC4	GC5	GC6	Total
1965							3.01
1966	3.44	1.67	6.25	7.69	4.72		4.58
1967	2.29	6.67	12.50	5.77	4.25		5.23
1968	3.44	8.33	8.33	7.69	3.30		5.01
1970	8.05	10.00	14.58	10.96	6.85	5.00	8.98
1971							11.47
1972							12.47
1973							9.48
1974	5.74	12.50	23.96	11.64	10.27	13.33	11.97
1975	10.34		8.33				9.63
1978	9.77	8.33	17.71	15.07		13.33	12.50
1979	10.92	10.83	18.75	12.33		13.33	12.80
1980	7.47	5.83	14.58	12.33		8.33	9.45
1981	4.02	4.17	12.50	8.22		8.33	6.99

P>0.05) (Fig. 3). Since density of females varied between sections, combining results from these sections could potentially mask a relationship between density and production in these smaller divisions of the population. However, there was no significant difference in production between the sections (Kruskal-Wallis test, P>0.05) and production was not inversely related to density on any of the sections (Fig. 4).

Age Structure

In all years combined, proportionately fewer yearlings than adults had broods overall (Chi^2=4.434, P<0.05) and fewer yearlings than adults had broods aged 4 or more weeks (Chi^2=6.441, P< 0.01) (Table 4). However, yearlings with broods were as successful as adults in raising juveniles to age 4 or more weeks (Chi^2=0.099, P>0.05)(Table 4). Combining all years, brood size when juveniles were aged 0-4 days was smaller for yearlings than adults (t-test, 1-tailed; t=1.668, P<0.05) (Table 5). When juveniles were aged 4 or more weeks, brood size of yearlings was not smaller than that of adults in all years combined (t-test, 1-tailed; t=1.319, P>0.05); but because more adults than yearlings have broods, the number of juveniles aged 4 or more weeks per adult was greater than that per yearling (paired t-test, 1-tailed; t=-3.558, P<0.01)(Table 5).

Since fewer yearlings than adults had broods and consequently were less productive than adults, the influence

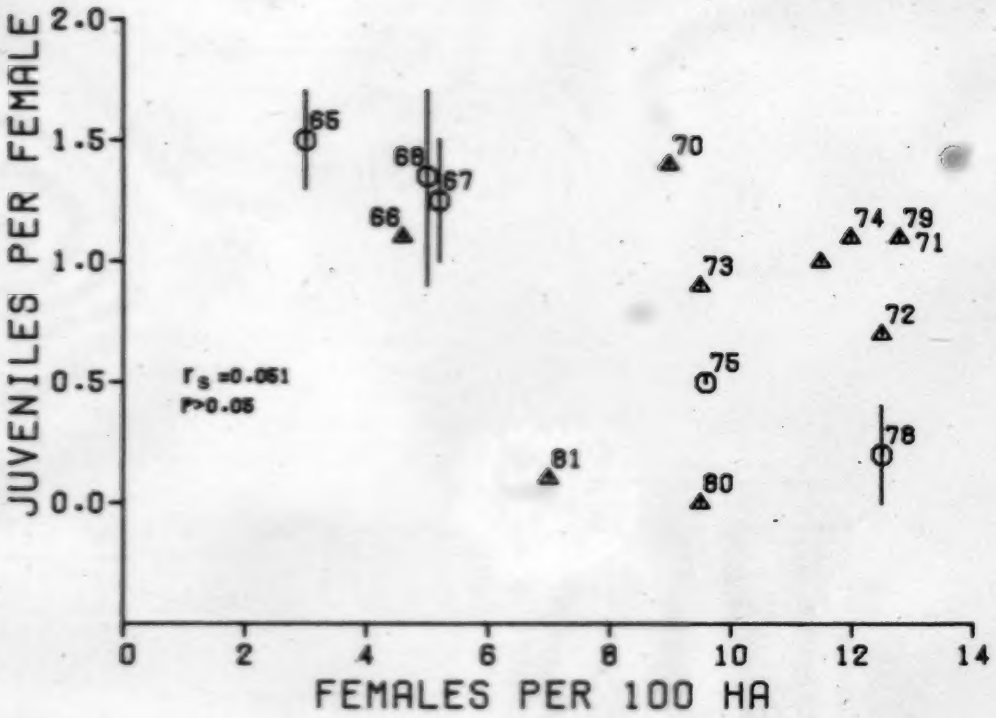

Figure 3. Relationship between number of juveniles aged 4 or more weeks per female and density of resident females (1965, 1967, 1968, 1975, and 1978 presented for comparative purposes, but not included in correlation analysis - see methods).

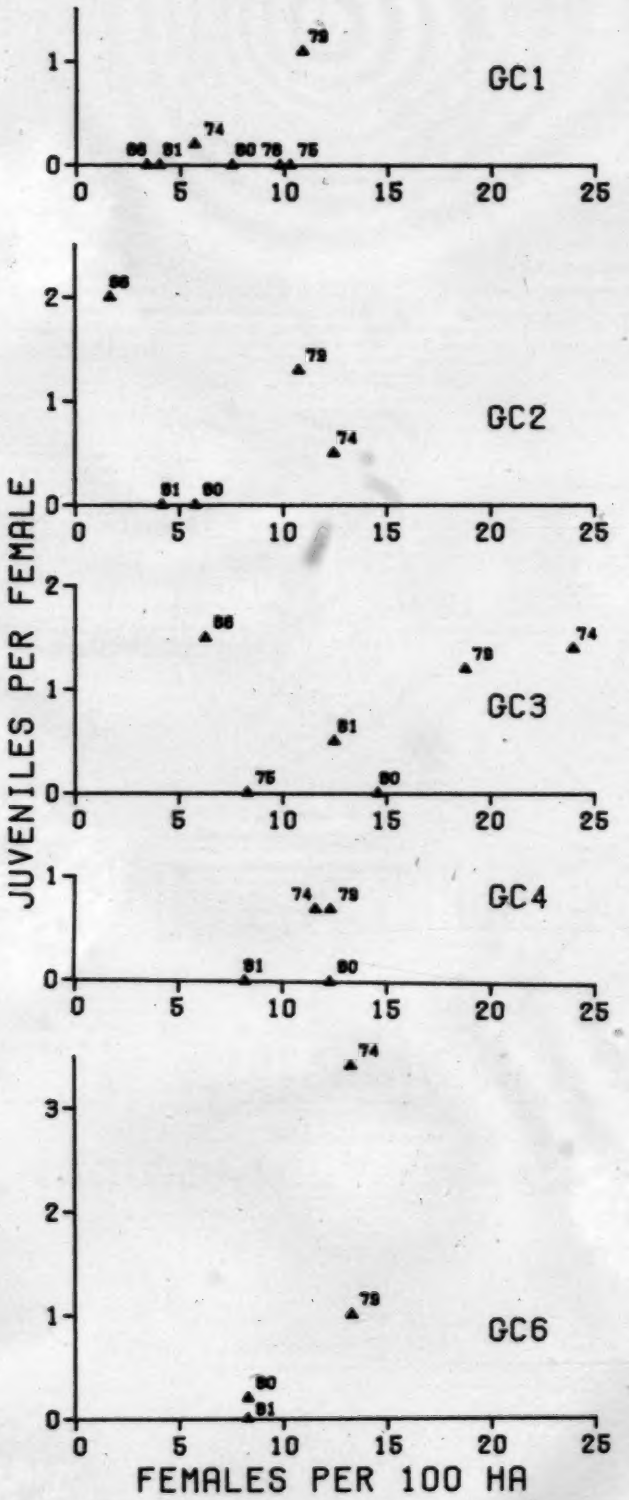

Figure 4. Relationship between number of juveniles aged 4 or more weeks per female and density of females on sections GC1-GC4 and GC6 of the study area.

Table 4. Number of females resident on the study area, number with broods, and number with broods aged 4 or more weeks for the years 1965-1968, 1970-1975, and 1978-1981.

	Resident females[1]		Females with broods		Females with broods aged 4 or more weeks	
Year	Adult	Yearling	Adult	Yearling	Adult	Yearling
1965[2]	5(56)	4(44)	5	1	5	1
1966	15(71)	6(29)	7	2	7	2
1967	15(63)	9(37)	6	4		
1968	11(48)	12(52)	5	6		
1970	28(78)	8(22)	14	2	11	2
1971	25(54)	21(46)	10	7	9	4
1972	31(62)	19(38)	15	1	12	1
1973	26(68)	12(32)	9	6	7	4
1974	28(58)	20(42)	13	9	10	7
1975[3]	11(46)	13(54)	3	0	3	0
1978	28(68)	13(32)	7	2		
1979	31(74)	11(26)	15	4	15	3
1980	23(74)	8(26)	3	0	1	0
1981	22(95)	1(5)	5	0	2	0
Total	299	157	117	44	82	24

[1]Percent in parentheses.
[2]Based on complete census of two sections (GC1 and 5).
[3]Based on complete census of two sections (GC1 and 3) and incomplete census of three sections (GC2, 4, and 6).

Table 5. Number of juveniles per female in broods of known size and aged 0-4 days and 4 or more weeks, and number of juveniles aged 4 or more weeks per resident female for the years 1965-1968, 1970-1975, and 1978-1981.

	Juveniles per brood female						Juveniles per resident female		
	0-4 days			4 or more weeks			4 or more weeks		
Year	Adult	Ylg	Total	Adult	Ylg	Total	Adult	Ylg	Total
1965[2]				3.0 n=3	3.0 n=1	3.0 n=4			(1.3-1.7)[1]
1966	4.7 n=4		4.7 n=4	2.7 n=7	2.0 n=2	2.6 n=9	1.3	0.7	1.1
1967	4.7 n=4	4.0 n=1	4.6 n=5	4.0 n=3	3.3 n=4	3.6 n=7			(1.0-1.5)[1]
1968	5.0 n=3	3.0 n=3	4.3 n=6	5.0 n=2	3.3 n=3	4.0 n=5			(0.9-1.7)[1]
1970	4.4 n=7		4.4 n=7	3.1 n=11	3.0 n=2	3.1 n=13	1.5	0.8	1.4
1971	5.0 n=12	4.0 n=8	4.6 n=20	3.1 n=9	1.8 n=4	2.6 n=13	1.2	0.6	1.0
1972				2.1 n=12	2.0 n=1	2.1 n=13	1.0	0.1	0.7
1973				2.6 n=7	1.6 n=4	2.3 n=11	0.9	0.8	0.9
1974	4.6 n=7	4.0 n=4	4.4 n=11	2.5 n=13	2.4 n=9	2.5 n=22	1.1	1.1	1.1
1975[3]	4.3 n=3		4.3 n=3	4.0 n=3		4.0 n=3	1.1	0.0	0.5
1978	3.2 n=4	5.0 n=1	3.6 n=5	0.0 n=2	0.0 n=1	0.0 n=3			(0.0-0.4)[1]
1979	5.7 n=4		5.7 n=4	2.5 n=15	1.8 n=4	2.4 n=19	1.2	0.6	1.1
1980	5.0 n=2		5.0 n=2	0.3 n=3		0.3 n=3	0.0	0.0	0.0
1981	3.5 n=2		3.5 n=2	0.6 n=5		0.6 n=5	0.1	0.0	0.1

[1]Range estimated (see methods).
[2]Based on complete census of two sections (GC1 and 5).
[3]Based on complete census of two sections (GC1 and 3) and incomplete census of three sections (GC2, 4, and 6).

of annual change in age structure on production each year was examined. The relationship between the proportion of yearlings in the population and the number of juveniles aged 4 or more weeks per resident female was not significant (Spearman's $r=-0.037$, $P>0.05$) when all years were considered (Fig. 5). However, removal from the analysis of data for 1980 and 1981, when neither adults nor yearlings were productive, resulted in a significant negative correlation (Spearman's $r=-0.731$, $P<0.05$).

Timing

Timing of hatch, based on median hatch date, differed among years (median test, $P<0.0001$) (Table 6). Both first-known (paired t-test, 1-tailed; $t=5.603$, $P<0.01$) and median (paired t-test, 1-tailed; $t=3.404$, $P<0.01$) hatch dates were earlier for adult than for yearling spruce grouse (Table 6). However, the proportion of yearlings in the population was not correlated with median hatch date for the whole population each year (Spearman's $r=0.434$, $P>0.05$) (Fig. 6). Therefore age structure in this population did not appear to affect the timing of hatch.

First-known hatch date of all females was not correlated with maximum or minimum temperature, average precipitation, or number of days with precipitation in any 7-day period from 1 April to 9 June. Median hatch date was not correlated with average precipitation or number of days with precipitation in any of the same periods. However,

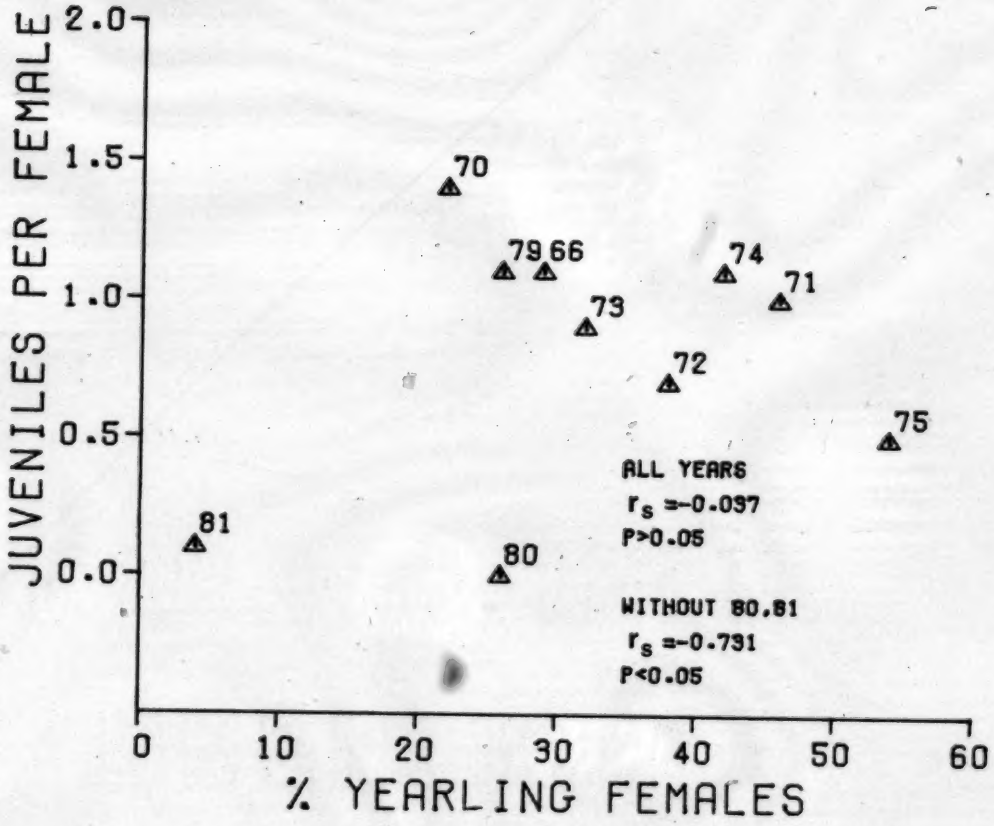

Figure 5. Relationship between number of juveniles aged 4 or more weeks per female and proportion of yearling females in the population.

Table 6. Timing of reproductive events as estimated by the median date of rapid ovarian recrudescence, first known hatch date, and median hatch date for the years 1965-1968, 1970-1975, 1978-1981[1].

Year	Median rapid recrud-escence	First hatch date			Median hatch date		
		Adult	Ylg	Total	Adult	Ylg	Total
1966	22May n=8	22Jun n=7	1Jul n=1	22Jun n=8	28Jun n=7		28Jun n=8
1967	31May n=10	28Jun n=6	6Jul n=4	28Jun n=10	1Jul n=6	8Jul n=4	8Jul n=10
1968	24May n=10	26Jun n=6	28Jun n=4	26Jun n=10	30Jun n=6	7Jul n=4	1Jul n=10
1970	22May n=16	25Jun n=14	29Jun n=2	25Jun n=16	28Jun n=14		29Jun n=16
1971	21May n=23	18Jun n=14	24Jun n=9	18Jun n=23	27Jun n=14	29Jun n=9	28Jun n=23
1972	23May n=17	20Jun n=16	3Jul n=1	20Jun n=17	30Jun n=16		30Jun n=17
1973	21May n=20	24Jun n=15	27Jun n=5	24Jun n=20	28Jun n=15	1Jul n=5	28Jun n=20
1974	28May n=23	29Jun n=15	1Jul n=8	29Jun n=23	6Jul n=15	5Jul n=8	5Jul n=23
1975	24May n=18	22Jun n=10	29Jun n=8	22Jun n=18	28Jun n=10	1Jul n=8	1Jul n=18
1978	25May n=8	24Jun n=6	4Jul n=2	24Jun n=8	1Jul n=6		2Jul n=8
1979	21May n=19	18Jun n=15	3Jul n=4	18Jun n=19	28Jun n=15	5Jul n=4	28Jun n=19
1980	13May n=8	14Jun n=7	21Jun n=1	14Jun n=8	20Jun n=7		20Jun n=8
1981	23May n=5	29Jun n=5		29Jun n=5	30Jun n=5		30Jun n=5

[1]1975 and 1980 include hatch dates of females found within 5 km of study area.

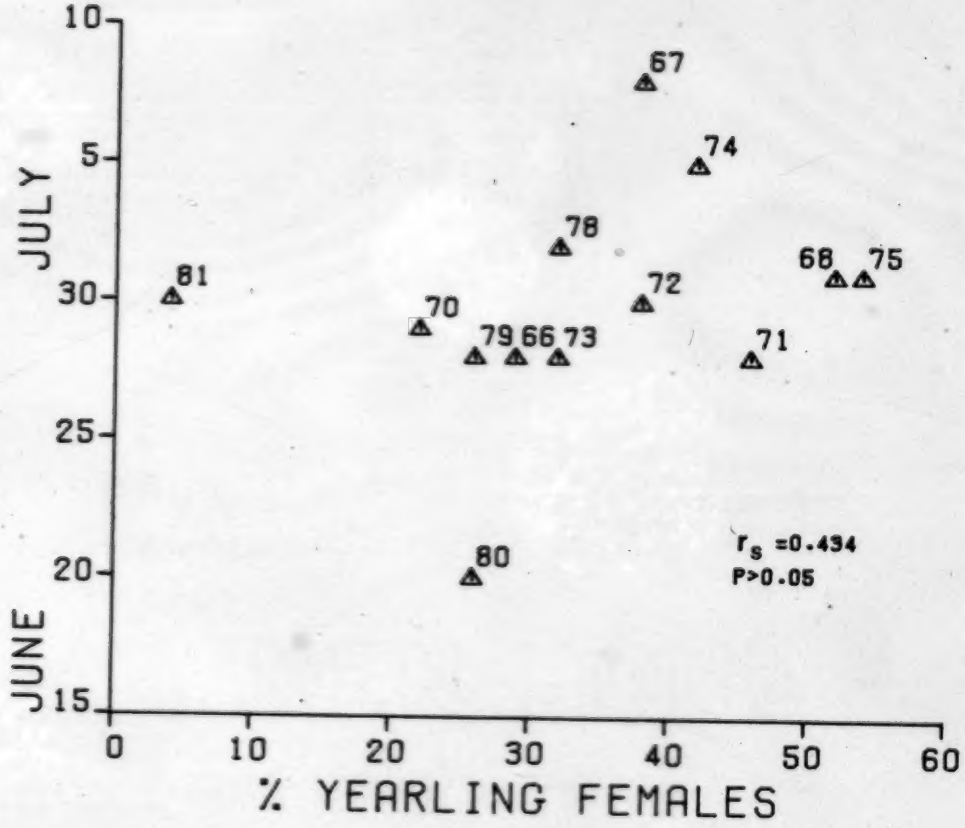

Figure 6. Relationship between median hatch date and proportion of yearling females in the population.

median hatch date was negatively correlated (Pearson's product-moment correlation) with temperature during two periods: with both maximum ($r=-0.679$, $P<0.05$) and minimum ($r=-0.714$, $P<0.01$) temperature from 29 April to 5 May and with maximum temperature 6-12 May ($r=-0.575$, $P<0.05$) (Fig. 7 and 8). Thus, maximum temperature in the 2-week period between 29 April and 12 May and minimum temperature from 29 April to 5 May appeared to be the major weather variables influencing the date prior to which 50% of nests hatch. However, since 50 correlations were calculated, 2.5 of these could be expected to be significant by chance alone at $P<0.05$. Therefore, although the three significant relationships that were found seem to have biological meaning (see Discussion), the possibility that they are due to chance must be noted.

By backdating from hatch date, the time and therefore the environmental temperature at which rapid recrudescence of follicles began each year can be determined. The estimated time required for development of ova from the beginning of rapid recrudescence to hatch (38 days) was subtracted from the median hatch date each year to give an estimate of the median date at which rapid recrudescence began. In what years did the time of rapid recrudescence approach 29 April to 12 May, the period for which maximum temperature was correlated with median hatch date?

Only in 1980 did timing of median rapid recrudescence approach 29 April to 12 May (Table 6). Maximum daily

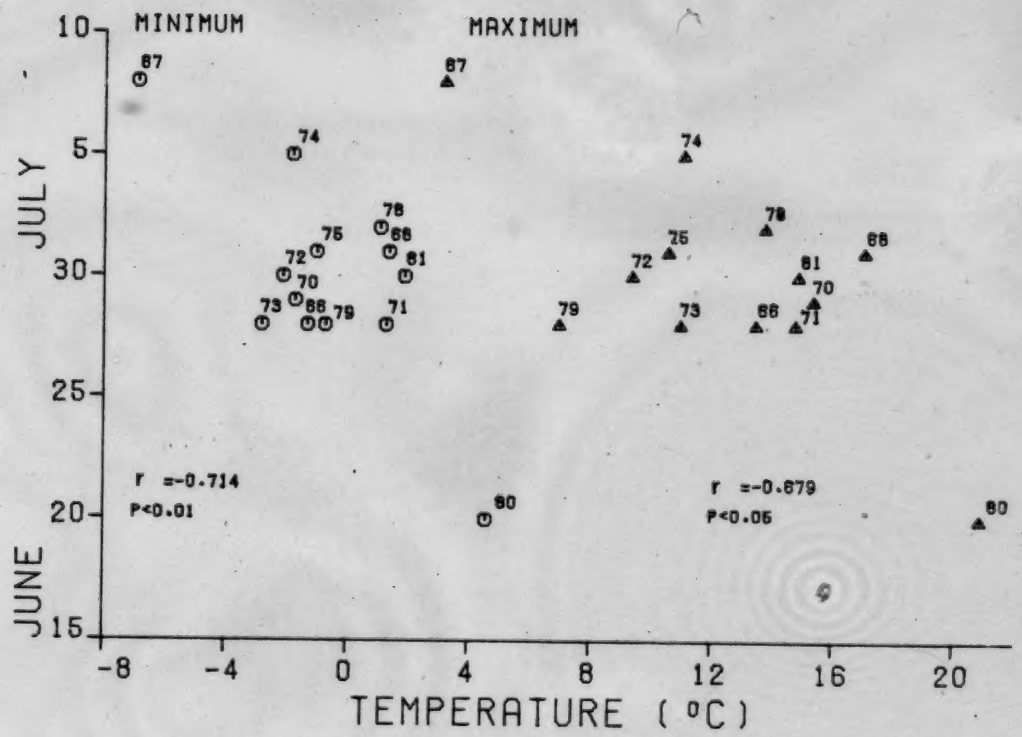

Figure 7. Relationship between median hatch date and maximum and minimum temperature, 29 April to 5 May.

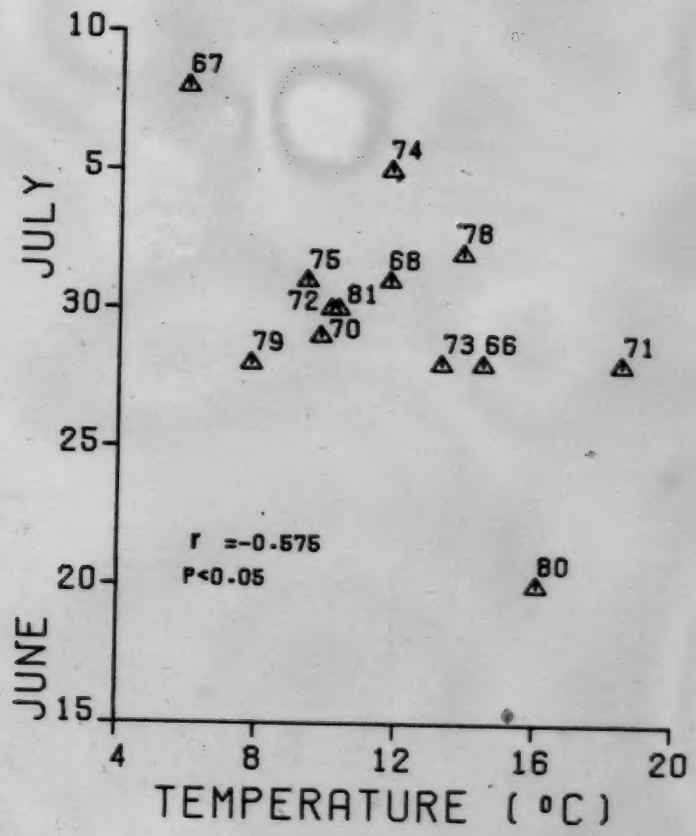

Figure 8. Relationship between median hatch date and maximum temperature, 6 to 12 May.

temperature reached 10°C or more on all days between 29 April and 12 May in only 2 of the years examined--1978 and 1980. That the estimate of median rapid recrudescence did not approach 29 April to 12 May in 1978 suggests that magnitude in addition to duration of high temperature is important. Average maximum temperature was higher in 1980 (18.5°C) than in 1978 (13.8°C) (Table 7) and median date estimated for the start of rapid follicular development was earlier (13 and 25 May, respectively; Table 6).

Perhaps early in May maximum temperature must not only be very high, but must also remain high for a longer period of time than later in May in order for rapid ovarian development to be stimulated. This is supported by a negative correlation between the number of consecutive days after 29 April and immediately before the median date of rapid recrudescence that maximum temperature remained ≥10°C and the number of days after 29 April that median development is estimated to have begun (Spearman's $r=-0.556$, $P<0.05$)(Fig. 9).

The influence of timing of hatch on annual variations in production was examined for each age class and for all females combined. There was no correlation between number of juveniles produced per adult and median (Spearman's $r=-0.072$, $P>0.05$) or first hatch dates (Spearman's $r=0.049$, $P>0.05$) of adults; or between number of juveniles produced per yearling and median (Spearman's $r=0.167$, $P>0.05$) or first hatch dates (Spearman's $r=0.406$, $P>0.05$) of yearlings.

Table 7. Average maximum temperature at Turner Valley, Alberta from 29 April to 12 May for the years 1966-1968, 1970-1975, and 1978-1981.

Year	Maximum temperature, °C 29April-12May
1966	14.0
1967	4.5
1968	14.4
1970	12.6
1971	16.7
1972	9.7
1973	12.1
1974	11.5
1975	10.0
1978	13.8
1979	7.4
1980	18.5
1981	12.6

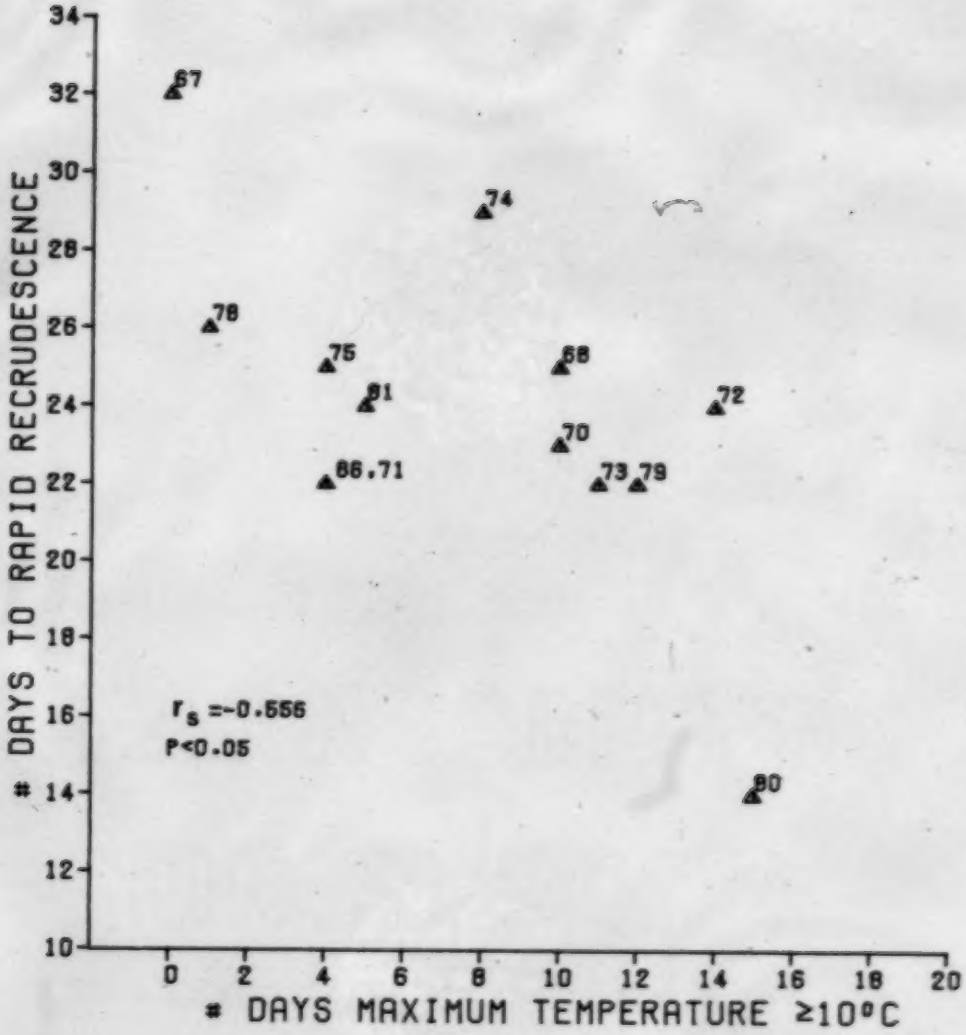

Figure 9. Relationship between number of days after 29 April and immediately before the median date of rapid ovarian recrudescence that maximum temperature was ≥10°C and the number of days between 29 April and the estimated median date of rapid recrudescence.

(Fig. 10). Since there was no difference in production between years with early and later median and first hatch dates for either age class, variations in production would seem to be unrelated to differences in timing of nesting between adults and yearlings.

When both age groups were combined, production was similarly unrelated to timing of hatch. The median hatch date each year of all females was not correlated with the number of broods seen on the study area (Spearman's $r=0.180$, $P>0.05$) or combined adult-yearling production (Spearman's $r=0.064$, $P> 0.05$) that year (Fig. 11). Furthermore, brood size at age 4 or more weeks was not different (t-test, 2-tailed; $t=0.758$, $P>0.05$) in broods hatched on or before the median hatch date and those hatched after that date when all years were combined.

Weather

None of the weather parameters examined for the periods 14 days before laying, during laying, and 1-14 days after hatch were correlated with proportion of females with broods or with brood size. However, significant correlations were found between three measures of reproductive success and weather during incubation and/or 1-4 days after hatch. The proportion of hens seen with broods was negatively correlated with the proportion of days with precipitation during incubation (Spearman's $r=-0.651$, $P<0.05$)(Fig. 12). Brood size at 11-19 days of age was negatively correlated

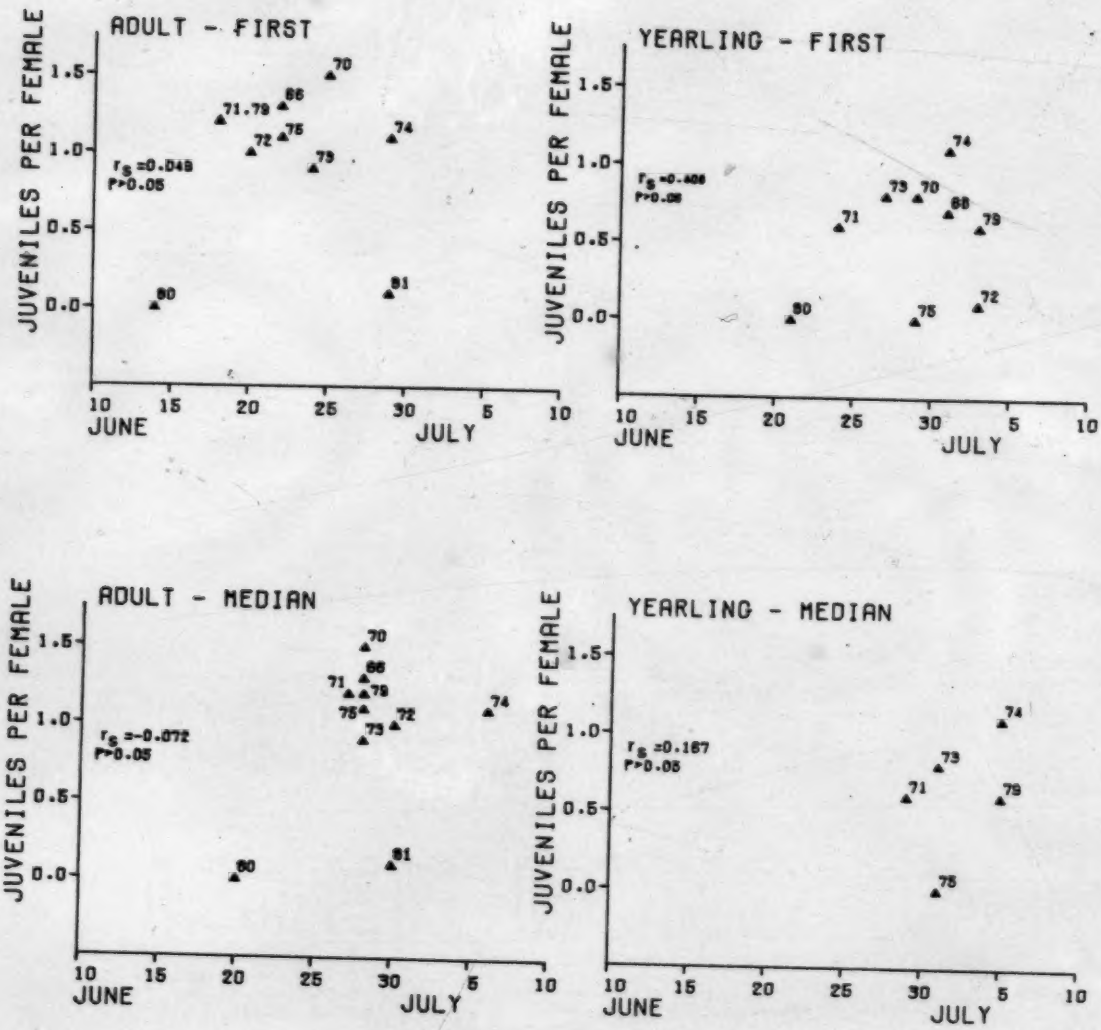

Figure 10. Relationships between number of juveniles aged 4 or more weeks per adult female and first and median hatch dates of adults and between number of juveniles aged 4 or more weeks per yearling female and first and median hatch dates of yearlings.

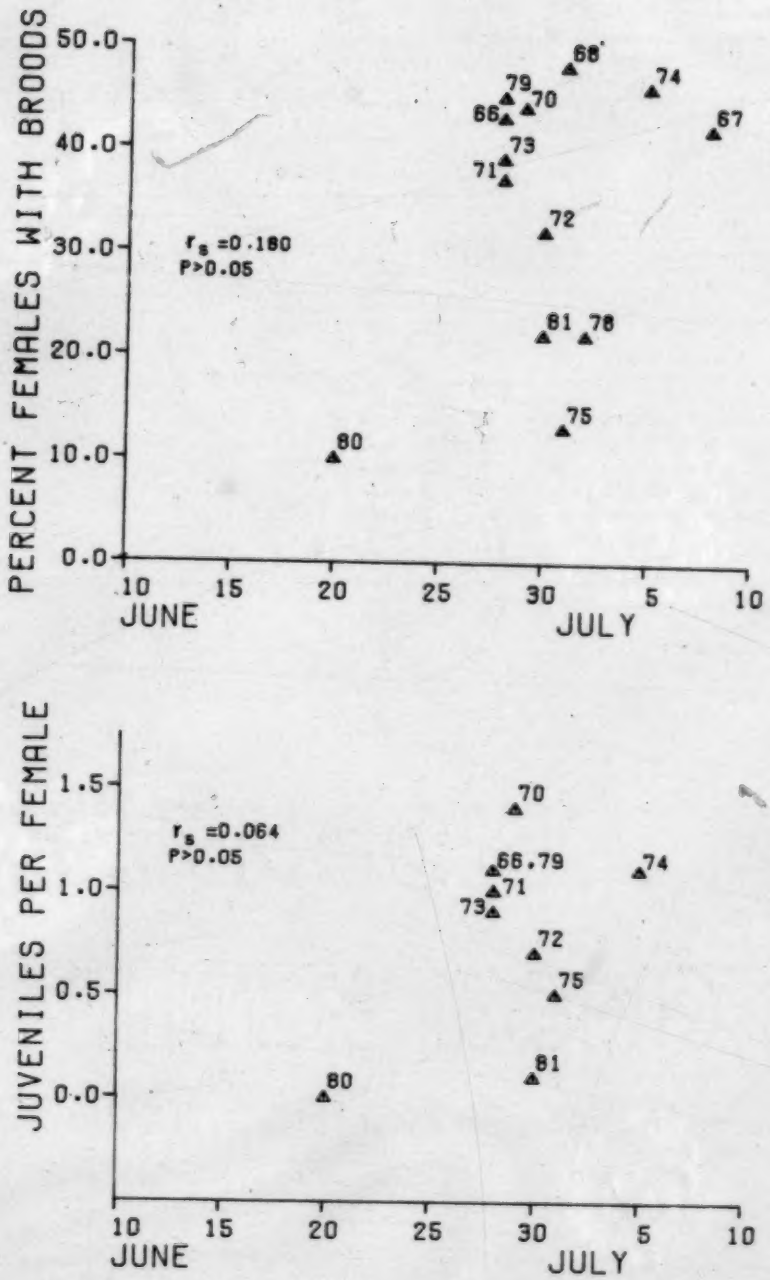

Figure 11. Relationships between proportion of females with broods, and median hatch date and between number of juveniles aged 4 or more weeks per female and median hatch date.

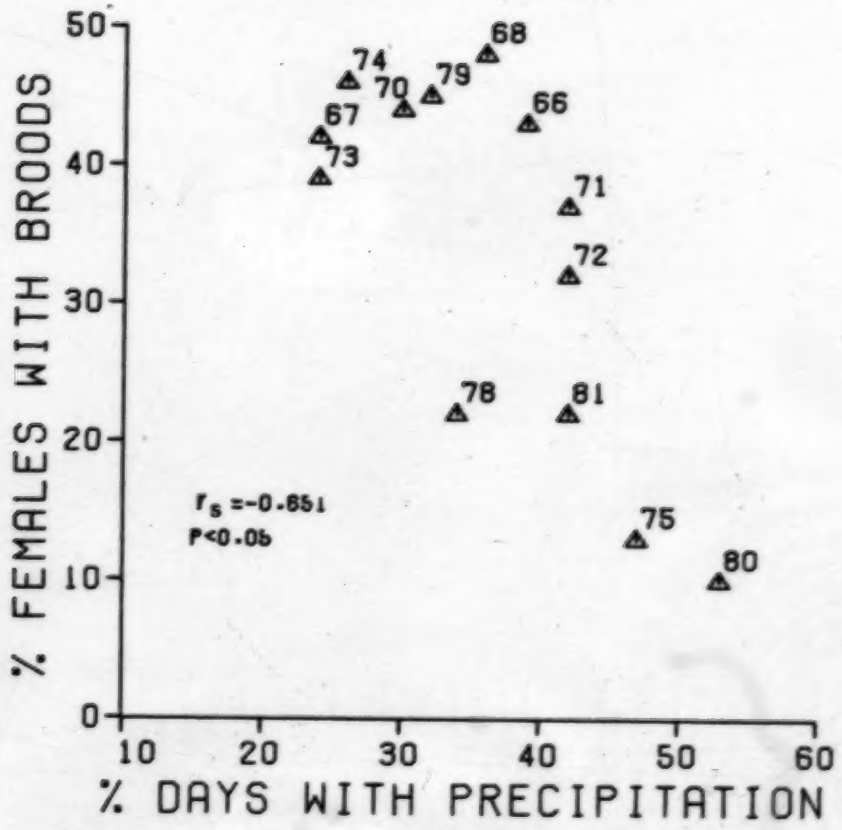

Figure 12. Relationship between proportion of females with broods and proportion of days with precipitation during incubation.

with maximum temperature 1-4 days after hatch (Spearman's $r=-0.714$, $P<0.05$)(Fig. 13). Whereas weather (maximum temperature) 1-4 days after hatch was correlated with a measure of reproductive success and weather 1-14 days after hatch was not, it is logical to assume that the influence of weather in the latter part of the 1-14 day period masked the earlier relationship. The influence of temperature 1-4 days after hatch, however, was only on brood size at age 11-19 days; production at age 4 or more weeks was not correlated with maximum (Spearman's $r=-0.327$, $P>0.05$) or minimum (Spearman's $r=-0.201$, $P>0.05$) temperature 4 days after hatch. Production was negatively correlated with the proportion of days with precipitation during incubation (Spearman's $r=-0.661$, $P<0.05$)(Fig. 14).

Since 60 correlations were calculated three could be expected to be significant by chance alone at $P<0.05$. Although the three that were found seem to have some biological meaning (see Discussion) the possibility that they were due to chance must be noted.

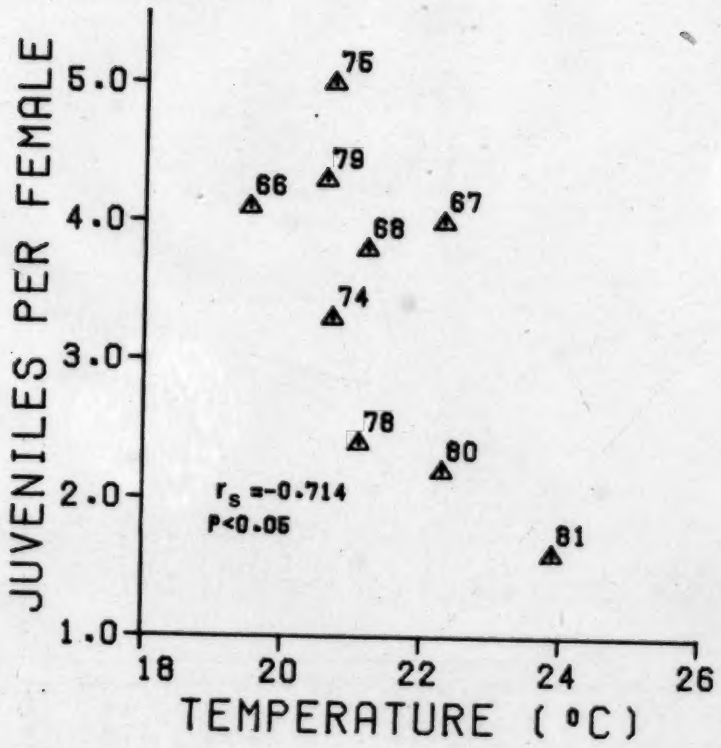

Figure 13. Relationship between brood size at age 11-19 days and maximum temperature the first 4 days after hatch.

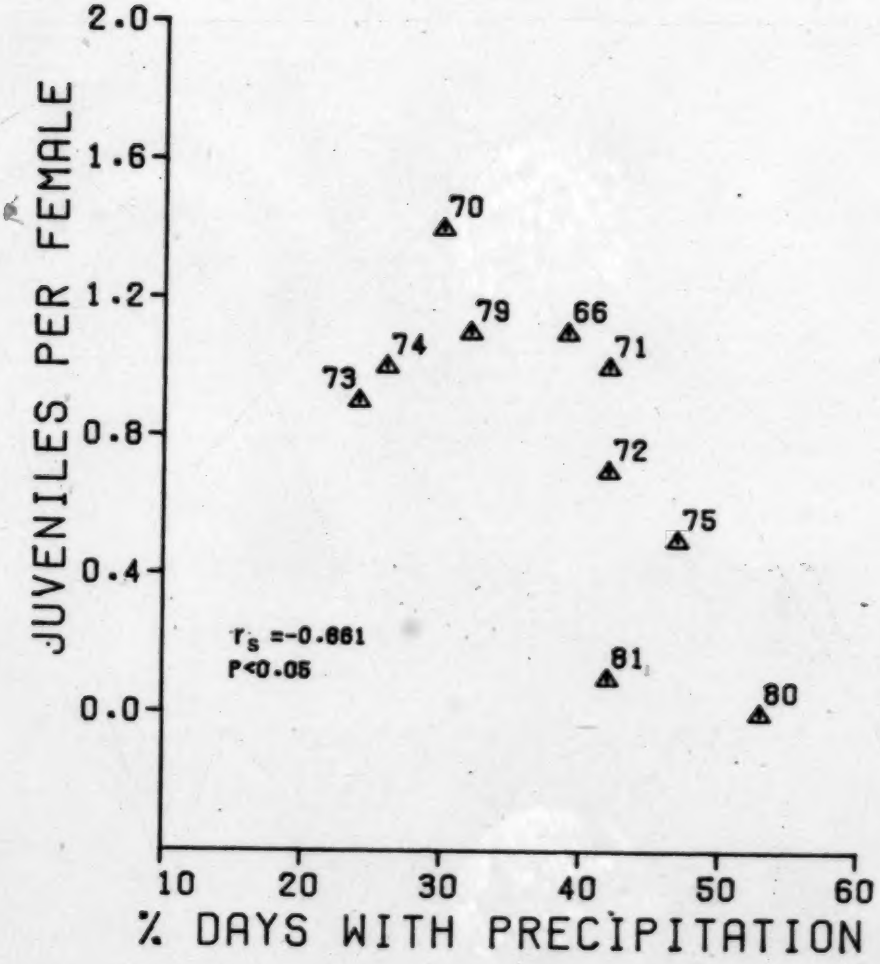

Figure 14. Relationship between number of juveniles aged 4 or more weeks per female and proportion of days with precipitation during incubation.

Discussion

Density

A reanalysis of the relationship between density and production of spruce grouse using data from additional years for the study area as a whole and its individual sections, did not support the negative relationship postulated by Boag *et al.* (1979) and hence the prediction made in this study. If there is a relationship between density and production as suggested by Boag *et al.* (1979), then other factors such as age structure of the female population and/or weather during incubation may act to modify it. Although density varied 4-fold during the years examined, the highest density reached on the study area as a whole was only 12.8 females per 100 ha. Density-dependent predation, the mechanism suggested by Boag *et al.* (1979), would not have an effect until a threshold density of grouse had been exceeded and predators were able to find an increased proportion of nests at higher densities. The threshold density at which the ability of ground-hunting predators such as coyotes (*Canis latrans*) to find nests is improved is not known and may be even higher than the densities of nesting females encountered.

Age Structure

Yearling female spruce grouse on the Gorge Creek study area are less productive than adults because fewer yearlings have broods. Two possible reasons for this are that not all yearlings attempt to nest as suggested for spruce grouse (Boag *et al.* 1979) and blue grouse (Hannon and Zwickel 1979), and that yearlings are less successful in incubating a clutch to hatching. Since the actual number of females that initiate a clutch of eggs is unknown, it is not possible to separate these possibilities.

Regardless of the cause of this difference in productivity, the influence of age structure on production, which in general seemed to decline with increased proportion of yearlings in the female population as predicted, would appear to have been overridden by the influence of other factors, especially in 1980 and 1981. Analysis of weather data would suggest that a high proportion of days with precipitation during incubation in 1980 and 1981 may have decreased production in those years to such an extent that a relationship between age structure and production was masked.

Timing

Timing of nesting is later for yearling than adult female spruce grouse, possibly because they are less physiologically mature than adults and hence establish territories later, or because they are inhibited from

breeding until after adults have nested as suggested for blue grouse (Zwickel 1977). Although physiological immaturity has not been investigated in spruce grouse, Hannon *et al.* (1979) found that yearling female blue grouse have smaller gonads than adults before, during, and after the breeding season, and suggested that delayed maturation and slower recrudescence of follicles may be responsible for later breeding in yearlings.

Yearling female spruce grouse start to defend territories about 2 months later than adults as evidenced by the time at which they first respond to taped female aggressive calls (Herzog and Boag 1977). Whether this difference is because adults retain the same territory from year to year while yearlings must first find a suitable unoccupied area on which to establish a territory or because yearlings become physiologically mature later is not known. That aggressiveness of resident adults may delay establishment of immigrants is suggested by the retreat of trespassers in response to aggressive calls and approach of territory holders (Herzog and Boag 1977). The chronology of aggressiveness, territory establishment, and reproductive maturity has not been documented; however, Hannon *et al.* (1982) present correlational evidence that physiological maturity of yearling female blue grouse is delayed by interactions with adult females. It seems probable that yearlings breed later than adults as a result of the combination of these social and physiological factors.

Although yearlings breed later than adults, timing of nesting for the population as a whole was not affected by the proportion of yearlings present each year. The influence of the adult segment on median hatch date would tend to mask that of the yearling segment: adults make up the majority (mean 66%) of the population in most years and are more likely to have broods.

Although photoperiod is the primary proximate factor controlling gonadal development in most temperate species (Immelman 1971), other conditions such as temperature must be sufficient for gonads to reach full functional maturity (Immelman 1973). If a threshold of ovarian development is reached in response to photoperiodic stimulation (Immelman 1973), the rate at which this development continues may be altered on a yearly or regional basis by environmental temperature. Garbutt (1979) found that the degree of inhibition of follicular development in ruffed grouse was dependent on temperature: very low temperatures (-23°C) had more effect than moderate temperatures (-3°C). This study suggests that a longer period of relatively high temperatures may be necessary to stimulate ovarian development early in May than may be necessary later in May. This appears to support Garbutt's (1979) conclusion that the timing of laying is determined by a combination of photoperiodic stimulation and temperature inhibition.

Although timing of nesting varied between years, contrary to my prediction, there was no relationship between

timing and number of females with broods or number of juveniles aged 4 or more weeks per female. Possibly the variation in timing of nesting is not sufficient to affect production. The variation in first-known hatch dates among years never exceeded 15 days and in 12 of 13 years 80% of the known hatch dates occurred within 14 days of the first hatch that year; in the remaining year this spread was only 17 days. Seasonal differences of this magnitude in weather or food supply may be too minor to influence reproduction. If conditions adequate for the survival of juvenile spruce grouse are met by the earliest time that hatching can occur and continue to be met through July and early August, production would not be expected to vary with time of hatch.

Weather

It has been suggested that variations in production ascribed to weather could be caused indirectly by energetic stress on incubating hens and reduced foraging time during adverse weather conditions, and directly by reduced thermoregulatory ability of newly hatched juveniles (Francis 1970, Theberge and West 1973, Myhre *et al*. 1975). Biebach (1979) found that the heat required for starlings (*Sturnis vulgaris*) to incubate a clutch of six eggs was a byproduct of metabolism between ambient temperatures of 12 and 20°C but between -10 and 12°C the metabolic rate was 25-30% higher than that of non-incubating birds. Vleck's (1981) data for zebra finches (*Poephila guttata*) were similar:

above the lower critical temperature (28°C) incubation cost was negligible but between 10 and 28°C the cost was a constant fraction (about 20%) of the metabolic rate of non-incubating birds.

Available data suggest that the lower critical temperature of tetraonids is lower than that of passerines; that of ruffed grouse in March was 0.3°C (Rasmussen and Brander 1973); of summer-acclimated willow ptarmigan, 7.7°C (West 1972); and of white-tailed ptarmigan (*Lagopus leucurus*) acclimated to 21°C, between 6.5 and 11.5°C (Johnson 1968). I found no data on the lower critical temperature of spruce grouse but the metabolic rate of penned spruce grouse was similar to that of willow ptarmigan (112 and 120 kcal per day, respectively) (Ellison 1972). During incubation, minimum temperature near the study area averaged between 3.7 and 7.9°C in all years (Table 8) - at or below the lower critical temperature of summer-acclimated willow ptarmigan, a level at which incubation of eggs may start to have a metabolic cost above that of maintenance.

The influence of precipitation on the lower critical temperature and energetics of birds is not well documented. If low temperature causes some stress to incubating females, precipitation may aggravate this; years with many days of rain during incubation may be years in which energetic costs to nesting females are high and nesting success is reduced thereby decreasing the number of juveniles hatched. Although nest loss from desertion is not known to be high in spruce

Table 8. Weather for the period during which 80% of the females on the study area were estimated to be incubating clutches of eggs.

Year	Temperature, °C		% days with precipitation
	Maximum	Minimum	
1966	16.6	4.6	39
1967	18.7	5.5	24
1968	18.1	5.1	36
1970	21.1	7.9	30
1971	17.1	5.4	42
1972	18.9	6.1	42
1973	18.3	4.6	24
1974	20.8	6.7	26
1975	18.2	4.7	47
1978	21.2	6.5	34
1979	19.3	5.0	32
1980	16.8	5.6	53
1981	16.9	3.7	42

grouse in southwestern Alberta, it accounted for 3 of 7 unsuccessful nests of spruce grouse in New Brunswick (Keppie 1982). If energetically stressed females desert more readily than less-stressed females, this could exacerbate loss that occurred from other causes of which predation is thought to be most important (Keppie and Herzog 1978, Keppie 1982). Poor production in 1975 and 1980 may have resulted from this combination of minimum temperature near the assumed lower critical temperature and high precipitation during incubation by reducing the number of successful nests and therefore the number of juveniles hatched. These years had more days of precipitation during incubation than all other years (1980 significantly so, $Chi^2=4.057$, $P<0.05$) (Table 8). There were fewer females with broods in 1975 ($Chi^2=5.716$, $P<0.05$) and 1980 ($Chi^2=9.491$, $P<0.01$) and production was among the lowest recorded (Table 5).

Nest attentiveness, particularly during cold rainy weather, may influence the energetics of incubating females by affecting the quantity and quality of food consumed and hence available for metabolic processes. Spruce grouse spend about 93% of daylight hours on the nest (McCourt *et al.* 1973); similar results are reported for other tetraonids: 95% in white-tailed ptarmigan (Giesen and Braun 1979), 94.3% in willow grouse (Pulliainen 1978), and 95.1% in capercaillie (Lennerstedt 1966). During absences from the nest, the female must procure sufficient food to meet metabolic requirements for maintenance and for incubation if

the latter requires an additional output of heat.

Red grouse females ate heavier particles during incubation than before laying but had a reduced feeding rate; their total food consumption, although similar at other times, was only 75% that of cocks during incubation (Savory 1978). During incubation more energy may be required but less food is consumed to meet maintenance needs. At other times of the year red grouse females ate more on cold days (Savory 1975); since incubation would reduce foraging time, it may limit this possibility.

Although food consumption may be reduced in incubating females, if they are energetically stressed by periods of cold, wet weather, they may increase the number and/or length of feeding trips in order to consume more food and thereby decrease nest attentiveness. Nest attentiveness can influence the amount of cooling to which eggs are exposed and thus the energy required to reheat them. Egg temperature dropped an average of 6.8°C during the absences of capercaillie females (Lennerstedt 1966). Rewarming eggs has a greater energetic cost than maintaining them at a constant temperature; the metabolic rate of zebra finches increased 3-fold when attempting to warm cooled eggs (Vleck 1981). This increased energy expenditure may be related to increased blood flow to the brood patch and the tachycardia associated with it (Vleck 1981). The heart rate of incubating willow grouse increased 4-5 times that at rest when females returned to the nest from foraging (Gabrielson

and Steen 1979). Increasing length of time away from the nest and decreasing ambient temperature lengthened the period of tachycardia. Thus, increased energy deficit may occur in those years when incubating females are subject to thermal stress associated with cold and exceptionally wet conditions. This may reduce production through increased loss of nests to desertion and by increased susceptibility of females to predation or stress-related disease.

Most loss of juvenile tetraonids occurs in the first 14 days after hatch (Zwickel and Bendell 1967b, Keppie 1977, Erikstad 1979). Their thermoregulatory ability is not well-developed until about a week of age (Theberge and West 1973, Myhre *et al*. 1975, Allen *et al*. 1979). It was predicted that cold, wet weather soon after hatch would contribute to increased mortality among the young birds. The data for spruce grouse do not support this prediction and, in fact, suggest the opposite. During cold weather the need for additional warmth from the female in the form of brooding may influence the amount of time available for very young juveniles to forage. Zwickel (1967) found that blue grouse females spent significantly greater amounts of time brooding very young juveniles on cool, rainy days than on warm, drier days. Length of foraging periods was reduced when juvenile rock ptarmigan were young and the temperature was low (Theberge and West 1973). Boggs *et al*. (1977) also found that juvenile willow grouse had shorter foraging and longer brooding periods in poorer weather. Furthermore,

length of foraging periods increased and length of brooding periods decreased with age. Nevertheless, Theberge and West (1973) found that the minimum foraging time available under cold, wet conditions was sufficient for very young rock ptarmigan in Alaska to gather their full energy requirements without relying on energy stored in the yolk sac.

Gullion (1970) suggested that environmental and other stresses may result in mortality indirectly by increasing the susceptibility of grouse to predation. Young grouse are vulnerable to terrestrial predators during the first few days after hatch when they are flightless. Zwickel (1967) found that distance travelled by young broods on cool, rainy days was less than on warmer, drier days and that this was inversely related to time spent brooding. If the distance travelled is less and the female and brood spend more time clustered in each location, it is possible that on cool, rainy days broods leave fewer, shorter scent trails to attract ground hunting predators such as coyotes. Wells and Lehner (1978) reported that although coyotes use visual and auditory cues in locating prey when confined to a small area (30 m^2), olfactory stimuli may be more important on a larger area. Perhaps cool weather shortly after hatch increased the time spent brooding, decreased the length of scent trails and subsequently improved the survival of spruce grouse to age 11-19 days by reducing predation. Brood size at age 11-19 days was lowest in 2 years (1980 and 1981) of high average maximum temperature the first 4 days after hatch

(Table 9). In addition, only 10 and 22% of females had broods in each of these years respectively. This may reflect not only a decrease in the number of females attempting to nest and/or successful in hatching a clutch but also loss of complete broods too soon after hatch for their presence to have been detected.

Spring density of female spruce grouse did not appear to be an important variable influencing production of juveniles. In addition, production did not vary with time of hatch each year and was not related to maximum or minimum temperature, average precipitation, or proportion of days with precipitation before laying, during laying, or after hatching. However, production may have been related to the age structure of the population. Although there was no significant correlation between production and proportion of yearlings in the population, yearlings were less likely to have broods and production by yearlings was less than that by adults. A relationship between age structure and production may have been overridden by the effects of severe weather. Production was negatively related to the proportion of days with precipitation during incubation; however, this relationship was most apparent under extreme conditions and would appear to have little influence under the rather broad range of conditions encountered in most years. Although maximum temperature the first 4 days after hatch was negatively related to brood size at age 11-19 days, the influence of this factor was not apparent after juveniles

Table 9. Weather for the period which includes the time 80% of the broods on the study area were aged 0-4 days.

Year	Temperature, °C		% days with precipitation
	Maximum	Minimum	
1966	19.5	6.3	22
1967	22.3	6.1	6
1968	21.2	7.4	20
1970	21.9	8.1	33
1971	18.2	4.9	33
1972	17.0	5.3	56
1973	20.0	6.2	27
1974	20.7	6.5	33
1975	20.7	6.9	36
1978	21.1	8.2	50
1979	20.6	6.6	29
1980	22.3	8.0	33
1981	23.9	8.6	25

had reached 4 or more weeks of age. Possibly the proportion of females with broods was more important in determining the number of juveniles eventually produced than was early brood size.

There is some evidence to suggest that production influences population size the following spring in some tetraonids (Bergerud 1970, Myrberget 1972). This may simply be a result of variations in the number of juveniles available as potential recruits. However, juvenile spruce grouse produced on the Gorge Creek study area are only one source of potential recruits to the spring population. McKinnon (in prep.) found that the number of yearlings in the spring population at Gorge Creek was correlated with production the previous summer and discussed the possible influence of production on nearby areas on yearling population size. Since immigration from other areas accounts for an average of 60% of the male and 92% of the female yearlings in the population each spring (Keppie 1979), production on areas outside the study area is an important variable in determining the number of potential recruits to the Gorge Creek population.

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